# INTERNAL MOULD MARKINGS IN A CRETACEOUS AMMONITE FROM NIGERIA

*by* P. M. P. ZABORSKI

ABSTRACT. Linear and concentric markings are described from steinkerns of the Upper Cretaceous ammonite *Paravascoceras* from Nigeria. The markings are intimately associated with the lobules of the suture lines. They probably record adapical projections of a preseptal prismatic zone of shell material which were secreted by those parts of the mantle corresponding to the lobules during mantle translocation. The posterior mantle margin was under muscular attachment at these points during translocation and subsequent septal secretion. Translocation itself probably took place in two stages: an initial phase of rapid mantle movement during which liquid entering the new chamber space was derived from the main body tissues; and a second, longer, phase of gradual translocation during which existing cameral liquid was transferred to the new chamber space.

VARIOUS markings are known from ammonite internal moulds. Most are confined to the body chamber and have generally been interpreted as the sites of muscle attachments. The following four types of marking occur repeatedly:

1. A pair of symmetrically disposed tongue-shaped or circular impressions in the posterodorsal part of the body chamber (see Crick 1898, Jones 1961, Jordan 1968, Kennedy and Cobban 1976), usually interpreted as the scars of retractor muscles similar to those in *Nautilus* (see Mutvei 1957). Jordan (1968) and Bayer (1970) described an associated dark band running around the umbilical shoulders which they interpreted as marking the successive positions of these muscles during growth.
2. A small lobate or circular structure in the posteroventral part of the body chamber (see Jones 1961, Jordan 1968). Mutvei and Reyment (1973) suggested that a gill retractor muscle may have been attached here.
3. An annular elevation or elevations, often indicated by coloration, which encircles the adapical part of the body chamber (see Crick 1898, Jordan 1968). This feature has generally been compared with the annular elevation in *Nautilus* (see Mutvei 1957, 1964) which is the site for attachment of the longitudinal mantle muscles and the subepithelial muscles.
4. A pair of large, tongue-shaped lateral indentations in the body chamber and, less commonly, also on the phragmocone (see Jordan 1968), which are of uncertain origin.

In addition, Palframan (1969) described large, regularly shaped areas of coloration in the body chambers of *Hecticoceras*, again of uncertain significance. Phragmocone markings are usually confined to the siphonal region (see, for example, Grandjean 1910, Neaverson 1927, Hölder 1954, Birkelund 1965, Henderson 1984). They occur in two main forms, fine longitudinal grooves and ridges, the 'Haftstreifen' of Hölder (1954), and concentric striae which mirror the outlines of the sutural lobules, the 'Schleppstreifen' of Hölder (1954).

## PRESENT MATERIAL

The material described here comes from limestones in the uppermost Cenomanian to Lower Turonian Gongila Formation at Ashaka Quarry in north-east Nigeria (see Wozny and Kogbe 1983). A number of ammonite genera (*Vascoceras*, *Nigericeras*, *Paravascoceras*, *Paramammites*, *Thomasites*, *Pseudotissotia*, and *Wrightoceras*) occur here in extraordinary abundance, all as internal moulds in a similar state of preservation. Although vague indications are present in several of these genera, however, it is only in *Paravascoceras* that the markings described below can be positively identified.

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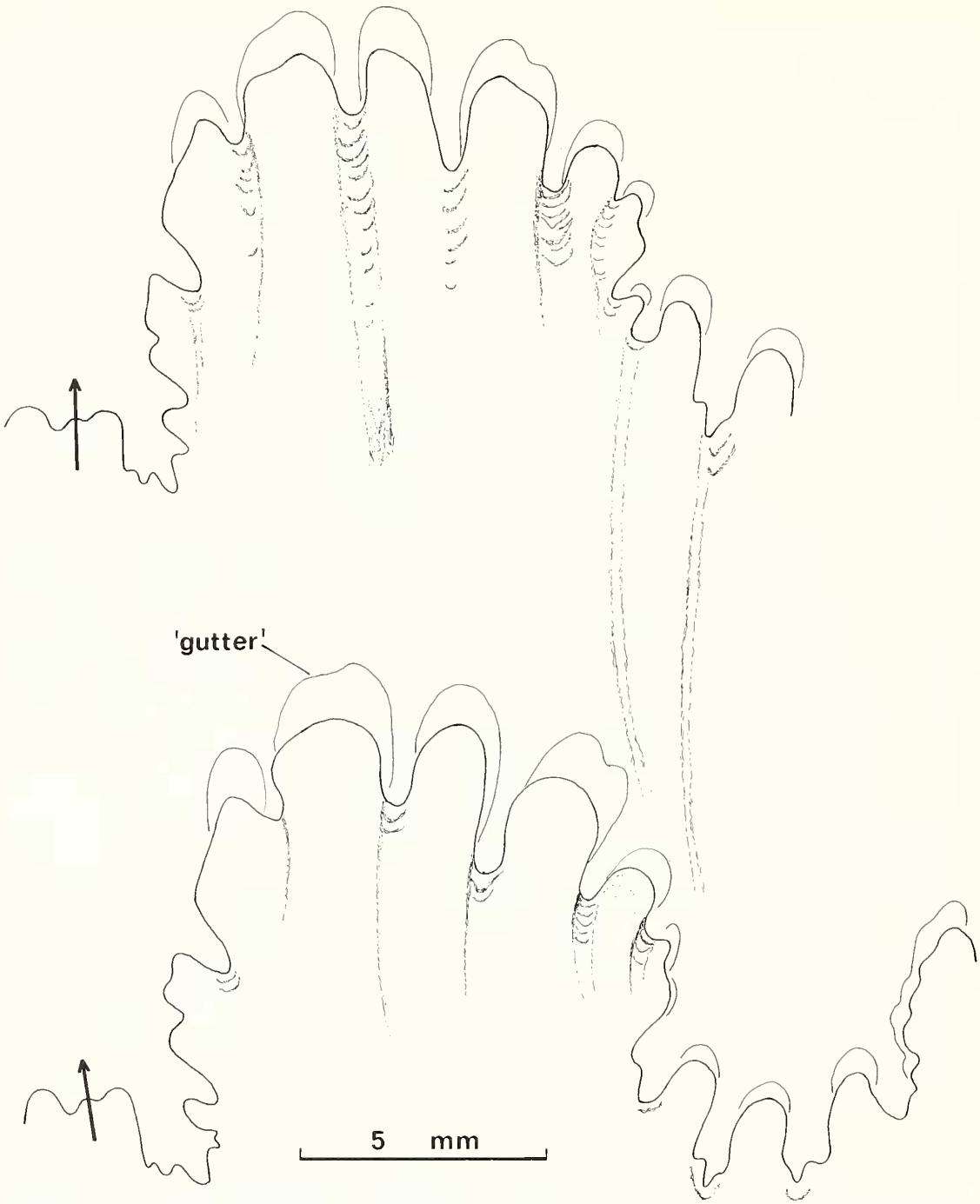
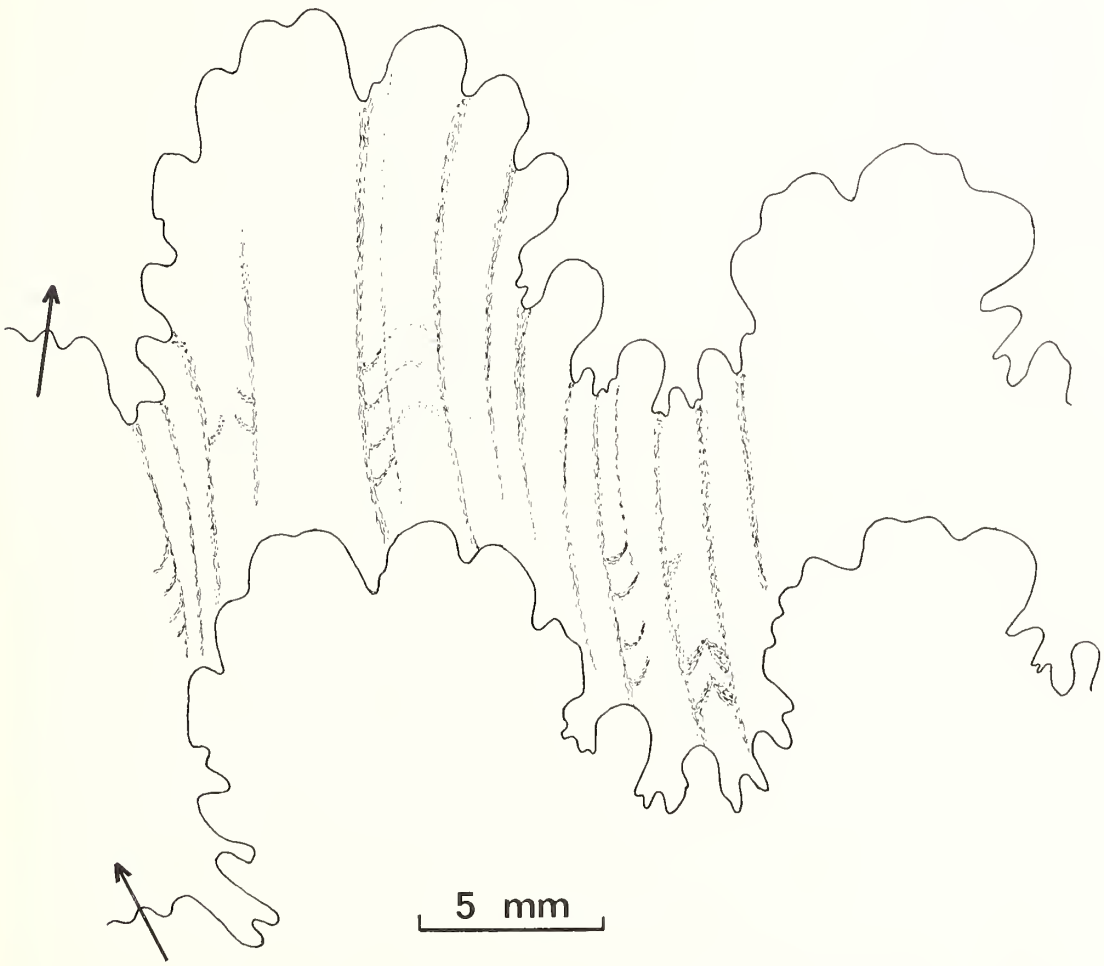



TEXT-FIG. 1. Two successive sutures in *Paravascoceras cauvini* (Chudeau) showing associated linear and concentric markings. In this specimen (BM (NH) C.90403) (see also text-fig. 3*d*) the linear markings are expressed in the form of faint grooves and the concentric markings as roughened or pitted areas on the mould surface. The 'gutter' is the mould of a postseptal prismatic zone of shell material (see Henderson 1984). Such a 'gutter' occurs frequently in many genera from Ashaka.

The specimens concerned are weakly ribbed, compressed to slightly depressed variants of *P. cauvini* (Chudeau 1909) (see also Schöbel 1975 for review and synonymy). They have been deposited in the Department of Palaeontology, British Museum (Natural History), London (register numbers C.90402–9). The most prominent markings displayed by these specimens are linear, spiral features (text-figs. 1–3) preserved in a number of ways: as bands of lighter or darker coloration; as very faint grooves; or as strips of surviving shell material. They occur upon the flanks, the venter, and the umbilical wall. Some extend the full distance between successive sutures (text-fig. 2) but many disappear adapically in a broad, annular area of coloration immediately adoral of the previous suture line (text-fig. 3*a*). Others can be traced only a short distance adapical of the suture line with which they are associated. In no case do these markings continue from chamber to chamber. Adorally they terminate at the lobules of the suture lines. Unlike forms of external spiral ornament, therefore, these linear features do not form regular, continuous spirals. Rather, each chamber contains its own association of these markings within which individual features frequently deviate slightly from a true spiral course. They do not reflect an external ornament such as strigation which might be displayed upon composite internal moulds (see McAlester 1962 for an account of this



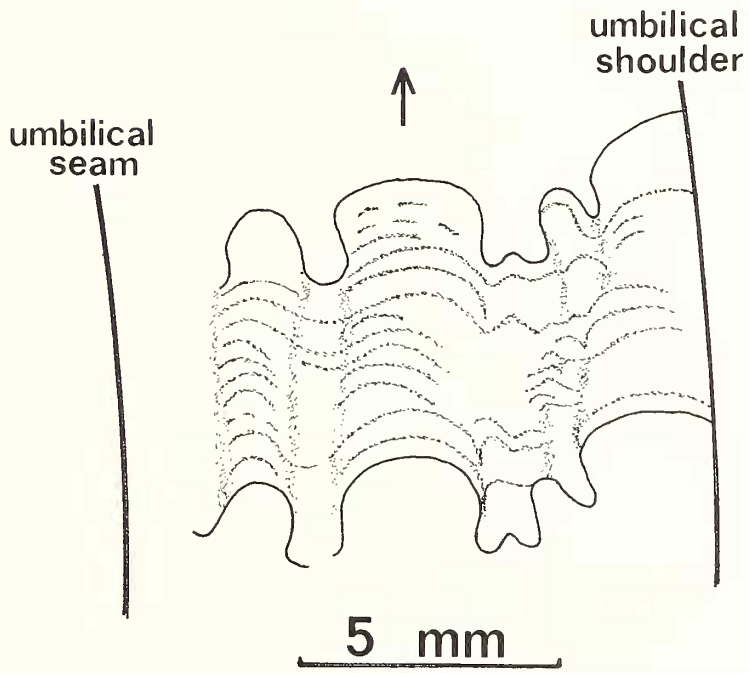

TEXT-FIG. 2. Two successive sutures in *Paravascoceras cauvini* (Chudeau) showing linear and concentric markings, expressed in this specimen (BM (NH) C.90404) as areas of lighter coloration on the mould surface.


TEXT-FIG. 3. Linear markings in *Paravascoceras cauvini* (Chudeau). *a–c*, specimen BM (NH) C.90402: *a*, ventral view ( × 2) also showing annular bands of coloration adoral of each suture line; *b*, *c*, ventral and lateral views ( × 1). In this specimen the markings are expressed in the form of bands of darker coloration or as strips of surviving shell material. *d*, specimen BM (NH) C.90403, in which the markings are expressed in the form of bands of darker coloration or as grooves on the mould surface (see also text-fig. 1). Both specimens uncoated

type of mould). Markings closely similar to those in *Paravascoceras*, however, have been described as 'Schleppstreifen der Lobenlinie' in the Triassic ceratites *Koninckites* and *Clypeoceras* by John (1909) and in the Lower Cretaceous ammonite *Polyptychites* by Vogel (1959, p. 509, text-fig. 14). Unfortunately, none of the present specimens has such markings preserved at the junction of the body chamber and phragmocone. In accordance with the explanation of their origin given below, however, they might be expected to extend into the non-adult body chamber for a distance not

exceeding the length of one phragmocone chamber. In particularly well-preserved specimens these linear features are associated with a series of concentric markings reflecting the outlines of the sutural lobules (text-figs. 1 and 2). The concentric markings are most obvious when the linear features are expressed in the form of grooves but they are always faint and frequently visible only with strong, oblique lighting. They generally take the form of roughened or pitted areas on the mould surfaces, but may also be indicated by coloration, and are usually best developed close to the suture lines. Similar markings ('Schleppstreifen') have been described from the siphonal region in several Jurassic and Cretaceous ammonites by Hölder (1954) and Birkelund (1965, p. 36). In rare Nigerian specimens these concentric markings may be contiguous with faint traces reflecting the outlines of the folioles, most commonly close to the suture lines but also around the umbilical area. One specimen (BM (NH) C.90409) shows a series of fine, darkly coloured bands upon the umbilical wall which reflect the entire outline of the suture (text-fig. 4). There are approximately fourteen successive bands within one chamber in this specimen. These markings are similar to the 'Pseudolobenlinie' described in *Koninckites* by Bayer (1977*a*, p. 327, fig. 15) and to the same features described by John (1909) in *Koninckites* and *Clypeoceras*.

Numerous specimens from Ashaka, belonging to several genera, show a relatively broad, darkly coloured band along the siphonal line. This feature is commonly present even when no other markings whatsoever are apparent. It is uncertain, therefore, whether it is related in any way to the markings described above. This siphonal marking is closely similar to the 'Dunkles Sipho-Band' described by Jordan (1968) and interpreted as marking the successive positions of a posteroventral muscle scar. Bayer (1974), however, believed that this dark band represented the area of attachment of siphuncle to shell, while Vogel (1959) thought a similar feature in *Polyptychites* to be a particularly prominent example of 'Schleppstreifen'.




TEXT-FIG. 4. Two successive sutures upon the umbilical wall in *Paravascoceras cauvini* (Chudeau) showing a series of darkly coloured bands reflecting the outline of the suture (specimen BM (NH) C.90409).

## INTERPRETATION

The linear markings described here in *Paravascoceras* are not continuous from chamber to chamber. The structures they reflect, therefore, appear to have formed in close association with the individual chamber in which they occur. As mentioned above, these markings may be preserved as surviving shell material, or as grooves upon the steinkerns which must also record the original presence of strips of shell material in contact with the inner shell wall and terminating at each septum. Henderson (1984, p. 477) described a band of prismatic shell material (the 'preseptal prismatic zone') preceding the septum proper in *Sciponoceras glaessneri* Wright. Although narrow and sharply defined along the folioles, this band of shell material is broader in the lobules and, here, extends adapically for a considerable distance in finger-like projections (see Henderson 1984, text-fig. 9*a*). It is probable that the linear markings in *Paravascoceras* record similar projections of a preseptal prismatic zone. Their associated concentric markings probably represent growth lines originally present upon these projections. If this interpretation is correct, these strips of shell material would have been secreted by those parts of the posterior mantle surface corresponding to the sutural lobules during mantle translocation. Hölder (1954, p. 374) and Vogel (1959, p. 509), following the proposal of John (1909, p. 35), also suggested that mantle translocation was responsible for the presence of 'Schleppstreifen'. In this context, it is instructive to examine chamber formation in the extant cephalopods *Nautilus* and *Spirula*.

### *Chamber formation in* Nautilus

Chamber formation and buoyancy control during this process in *Nautilus* have been described by Collins *et al.* (1980), Ward *et al.* (1981), and Ward and Chamberlain (1983). Chamber formation takes between 70 and 120 days in captive *N. macromphalus* and between 85 and 132 days in captive *N. pompilius*. In order to maintain buoyancy throughout its growth cycle, *Nautilus* retains liquid in the adoral chambers of the phragmocone which serves as a reserve of ballast. This liquid is slowly expelled to compensate for mass added to the animal through shell and soft tissue growth. The rate of liquid removal is extremely slow; Ward *et al.* (1981) showed that in aquarium-based *N. macromphalus* complete evacuation of a chamber takes as long as 135 days. Chamberlain and Moore (1982) found the constraining factor to be not the permeability of the siphuncular tube, but the rate of osmotic pumping. In fact, only in *Sepia* among living shelled cephalopods has short-term buoyancy control been observed; density changes in excess of 1 % can be effected in about six hours by varying the liquid : gas ratio of the cuttlebone (Denton and Gilpin-Brown 1973, p. 49). Ward (1979), Ward and Martin (1978), and Ward and Greenwald (1981) rejected the generally held view that *Nautilus* is able to vary its short-term buoyancy state in the same way; its rate of liquid exchange is far too slow for this. They noted that the animal maintains a very slight negative buoyancy and thought that it makes any vertical migrations by active swimming using the hyponome. Chamberlain's (1981) calculation that powered swimming would be a much more efficient method of effecting vertical migration than buoyancy adjustment fully supports this conclusion. Cameral liquid is essential, therefore, only to the growing animal; fully grown adults contain virtually none at all (Ward 1979, Collins *et al.* 1980), a slightly larger body chamber compensating for the extra buoyancy resulting from this. Translocation of the mantle during chamber formation is far more rapid than apertural growth. Only maximum estimates are available for the duration of translocation. As Henderson (1984, p. 475) noted, a maximum of 6 days can be inferred for one individual of *N. macromphalus* from the account given by Ward *et al.* (1981). In *N. pompilius* translocation phases are completed within maximum periods of 10–20 days (Ward and Chamberlain 1983). Actual translocation rates may be much faster than these timings suggest. In any event, it is known that translocation takes up a maximum of only 10 % of the entire chamber formation period. The migrating mantle leaves behind it a liquid which performs two functions: to support the newly forming septum until its calcification is well advanced; and to provide a reserve of ballast to be expelled during future growth at the aperture. This liquid is not sea water; although approximately isosmotic with sea water, its composition is different (Denton and Gilpin-Brown 1966). The liquid

must be derived from within the animal's soft tissues. There is some, inconclusive, evidence that translocation in *N. pompilius* is associated with unusual weight changes, perhaps caused by flooding of the new chamber space (Ward and Chamberlain 1983). This, if true, would suggest that expelled body fluid is rapidly replaced. Given the very low rates at which cameral liquid can be expelled, it is difficult to see how such weight changes would not result in buoyancy maintenance problems. A delay in the replacement of this body fluid might also have the result of bringing about a deflation of the body, thereby effecting the shortening of the body chamber which accompanies translocation (see text-fig. 5). Whatever the truth of this matter, there is a great disparity between rates of apertural growth and cameral liquid removal on the one hand, and rates of translocation and flooding of new chamber spaces on the other. This disparity requires that new cameral liquid be derived from the main body tissues.

*Chamber formation in* Spirula

In *Spirula* the shell is internal, there being no living chamber as such. The process of chamber formation has been described by Denton and Gilpin-Brown (1971) and Denton (1974). Each chamber space develops slowly and, as it does so, is filled with a clear liquid secreted by the body tissues which is isosmotic with sea water and the body fluids. In order to maintain buoyancy during shell growth, liquid is removed from the preceding chambers of the shell at the same time as the newly forming chamber space is being flooded. During evacuation of a chamber dissolved salts are first removed from the cameral liquid. The first liquid itself is only removed when the concentration of dissolved salts has fallen to about one-fifth that of sea water. The proportion of the overall cameral space occupied by liquid, however, remains much the same throughout the chamber formation cycle (see text-fig. 5).

*Chamber formation in* Paravascoceras

If the linear markings described here in *Paravascoceras* record the presence of adapical projections of a preseptal prismatic zone, then secretion of these structures and, consequently, mantle translocation, would appear to have been a gradual and incremental process. Translocation would not have been 'rapid' as in *Nautilus*, but, as in *Spirula*, a chamber space would have developed slowly. If this was so, then the mechanism of buoyancy control must also have differed from that in *Nautilus*. A gradual translocation would have required that, as in *Spirula*, cameral liquid was removed from completed chambers at the same time as the newly forming chamber space was being flooded. The liquid entering a new chamber could have been transmitted either directly from the posterior mantle surface or, alternatively, from the siphuncular tissue. As noted above, the osmolarity of the cameral liquid varies in successive chambers of the *Spirula* shell. This is also the case in *Nautilus* (Ward 1979). Its cameral liquid is initially isosmotic with sea water but the osmolarity is reduced during the early stages of chamber emptying, that is, prior to decoupling of the siphuncle and cameral liquid. After decoupling, however, the osmolarity increases. In view of these osmolarity changes in both *Spirula* and *Nautilus*, it is likely that a similar phenomenon prevailed in *Paravascoceras*. Liquid entering a new chamber space would have been isosmotic with the body fluids, thus precluding osmotic interchange with the posterior mantle surface. Liquid leaving the phragmocone, however, would have been hyposmotic to the body fluids. Transfer of liquid through the siphuncle from the phragmocone to a new chamber would, therefore, have required that parts of the siphuncular epithelium were absorbing liquid of low osmolarity while, simultaneously, the adoral part of the siphuncle was secreting liquid of higher osmolarity. It is not known whether any liquid is transferred to a new chamber through the siphuncle in *Spirula*. Denton and Gilpin-Brown (1971, pp. 370–371), however, thought it possible that the concentration of solutes might vary along its siphuncular epithelium. Diamond and Bossert (1968) suggested that the direction of water flow across a pumping epithelium would be reversible according to the direction of solute transport. As regards *Nautilus*, it is known that, if made artificially more buoyant, liquid can be returned to the camerae, its osmolarity, furthermore, corresponding to that of the liquid previously being removed from those camerae (Ward and Greenwald 1981). These factors suggest that transfer of liquid from

the phragmocone to a new chamber through the siphuncle may have been possible in *Paravascoceras*. During initial release of the mantle from the septum, however, expulsion of liquid from the main body tissues, directly from the posterior mantle surface, might have been necessary for the following reasons:

1. To maintain cameral liquid levels, as the chambers normally become increasingly voluminous during growth.

2. To bring about a partial deflation of the lobes, thereby aiding release of the posterior mantle surface from the septum. In *Paravascoceras*, as in the majority of ammonoids, the necks of the sutural lobes are constricted. Septal architecture, therefore, requires that some distortion of the soft tissues must have taken place upon mantle release. The septal surface in *Paravascoceras* is relatively simple and any lobe deflation would have needed only to be slight. It may, nevertheless, be significant that the linear markings described here frequently terminate adapically in a broad, annular band of coloration immediately adoral of the previous suture line (text-fig. 3*a*). If this colour band can also be taken as indicating the posterior mantle imprint, it would suggest a general loss of posterior mantle shape immediately upon release from the septum.

3. To produce a rapid, but short-lived, phase of mantle translocation which would have been necessary if apertural growth continued while the posterior mantle surface was stationary during septal secretion. This would have been the case even if, as suggested by Doguzhayeva (1982), apertural growth in ammonoids was slower during septal secretion. After this initial phase translocation would have been much slower. It would, in fact, have kept pace with apertural growth. If chamber emptying in *Paravascoceras* proceeded as in *Spirula*, it may have been during septal secretion, with the posterior mantle stationary, that dissolved salts were removed from the chamber being completed.

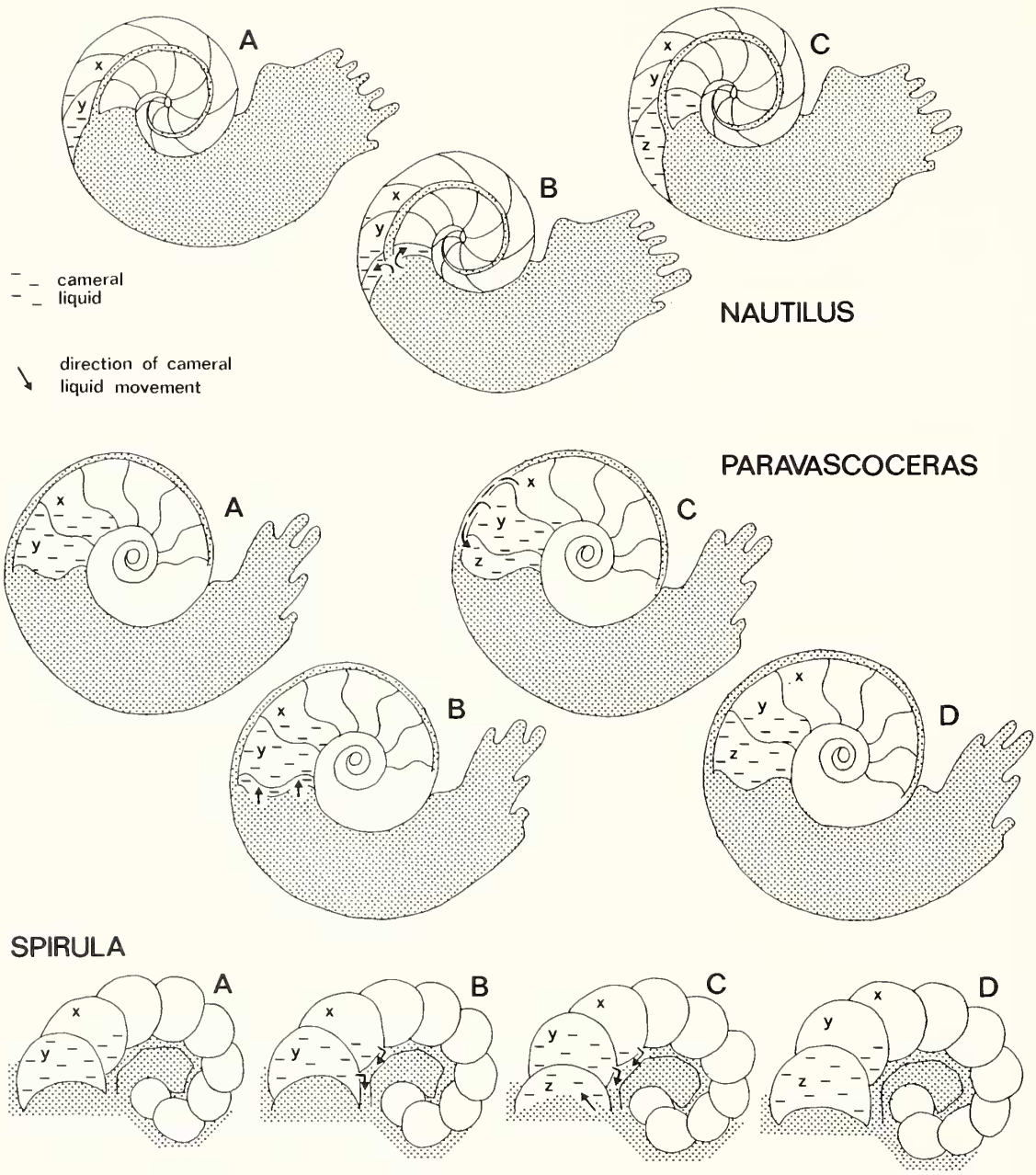
Clearly, the maximum possible rate of cameral liquid removal is a constraint upon the rate of apertural growth in *Nautilus*, but not upon the rate of mantle translocation. In *Paravascoceras*, however, the rate of cameral liquid redistribution would have been correlated with both rates of apertural growth and the largely synchronous process of mantle translocation. It may be mentioned that *Paravascoceras* was a shallow water genus of Tethyan distribution. In Nigeria it was a denizen of the trans-Saharan epeiric seaway which flooded northern Nigeria during the late Cenomanian and early Turonian. Water depths here are estimated as having averaged only 20–30 m (Petters 1978, Reyment 1980). On theoretical grounds, a mechanism of rapid buoyancy control would seem to have been superfluous to *Paravascoceras*. It is likely, therefore, that cameral liquid pumping rates were primarily matched with growth rates and were too slow for short-term buoyancy adjustment.

The gradual translocation phase envisaged here for *Paravascoceras* requires that the posterior mantle surface was unsupported by a septum for lengthy periods. In this case, a method of anchoring the posterior mantle surface during translocation would have been advantageous. The linear and concentric markings described here are intimately associated with the sutural lobules. The corresponding parts of the posterior mantle margin would, therefore, appear to have provided these attachment points, though specimens such as that shown in text-fig. 4 suggest that, in places, attachment was along a more continuous line. The linear markings in *Paravascoceras* are thought to represent adapical projections of a preseptal prismatic zone. Henderson (1984) suggested that this zone in *Sciponoceras* served as a temporary muscular attachment site for the perimeter of the posterior mantle surface immediately prior to secretion of the septum proper. He believed a second zone of prismatic shell, the 'postseptal prismatic zone', encircling the adoral face of the septum, provided a subsequent attachment surface until such time as translocation recommenced. Because, however, he regarded the septal periphery as the principal muscle attachment site in ammonites, Henderson (1984) suggested that bodily functions dependent upon the longitudinal musculature would have had to be suspended during translocation. He therefore concluded that translocation was accomplished very rapidly, perhaps taking only a few hours. Such a rapid translocation rate would imply either a mechanism of buoyancy control like that in *Nautilus*, or impossibly rapid rates of apertural growth and cameral liquid redistribution. The evidence provided by *Paravasco-*

*ceras* suggests that the adapical projections of the preseptal prismatic zone were secreted in increments by the mantle lobules during gradual translocation. The lobules would, therefore, have provided a series of temporary, presumably muscular, attachments throughout this lengthy period of mantle movement. The tenacity of such a form of attachment is, however, questionable. This suggests that the posterior mantle periphery was not the only, or even the principal, site of attachment. As Henderson (1984, p. 480) himself conceded, the various structures interpreted by Jordan (1968) as muscle scars may represent additional zones of attachment. Kulicki (1979) noted the metameric nature of the umbilical and ventral muscle(?) scars and took this fact to suggest a 'stepwise', rapid translocation pattern. Jordan (1968), however, found that these scars are frequently connected by darkly coloured bands which he regarded as marking the track of the relevant muscle attachments during translocation. The clarity of the scars at certain points within each chamber could be a reflection of the location of the muscles(?) during septal secretion when the mantle was stationary.

Seilacher (1973, 1975) and Westermann (1975*c*) have also attributed particular physiological significance to the lobe endings in ammonoids. Seilacher (1973, 1975) pointed out that the shape of the ammonoid suture could be explained by envisaging the existence of a number of 'tie-points' located at the tips of the lobules. The posterior mantle, initially with a planar form, was thought to have become strongly attached to the shell wall at successive 'tie-points' after translocation. Septal shape resulted from 'pull-off' or radial tension acting upon the septal mantle. Westermann (1975*c*) proposed that the posterior mantle surface in ammonoids consisted of an aponeurosis-like structure which retained much of the septal shape during translocation. While accepting that those parts of the mantle corresponding to the saddles, folioles, and associated flutes might have suffered some distortion during translocation, he believed mantle shape would have been maintained along the periphery of the lobes. Anteriorly the body would have been fastened at an annular elevation like that in *Nautilus*. During translocation the posterior aponeurosis would have slid along the shell wall until it reached the position of the new septum. Here it would have reaffixed itself, initially at the tips of the lobe incisions. Pressure of cameral liquid, transmitted adorally from the phragmocone, would have been a major factor causing reflation of the saddles, rather than 'pull-off'. This would also have produced adorally convex septa and prochoanitic septal necks. Finally, fixing of the entire mantle margin would have occurred, tightening in a radial direction extending the septal flutes, with septal secretion completing chamber formation. Westermann (1975*c*, text-fig. 7) (see also Ward and Westermann 1976) figured a suture in *Glyptoxoceras* in which the positions of the hypothetical 'tie-points' were normal but the lobules and folioles were reversed. This peculiarity was explained by envisaging a reversal of the direction of pressure applied to the posterior mantle surface during septal secretion. Bayer (1978), although suggesting a slow, 'creeping', method of translocation, denied the existence of 'tie-points', at least in the ontogenetic sense. He believed the reversed lobules of Westermann (1975*c*) to be distorted folioles resulting from the aberrant shaping of a planar posterior mantle surface. The specimens of *Paravascoceras* described here, however, provide evidence that posterior mantle shape was largely maintained during the greater part of translocation. Bayer (1977*a*) regarded the retention of posterior mantle shape during translocation as an exceptional circumstance. He found the 'Pseudolobenlinie' in *Koninckites* to be associated with fine ridges on the inner shell wall but regarded these as the result of abortive septal secretion following incomplete fastening of the septal mantle to the shell wall. John (1909), however, proposed that the various forms of 'Schleppstreifen' were connected with mantle growth and movement, more especially, with posterior muscle attachments concentrated in the lobes. He expressed surprise that soft tissues could leave such clear markings, but, as suggested here for *Paravascoceras*, these features probably mark the sites of myostracum.

The factor controlling chamber size in *Paravascoceras* remains uncertain. It may have been genetic, as suggested by Bayer (1977*b*) for cephalopods, related to the need for shell support by a septum, related to cameral liquid pressure, or perhaps related to siphuncular length. In regard to the last of these, Kulicki (1979) suggested that the connecting rings formed prior to translocation in ammonoids. This is not the case in *Nautilus* where calcification of the connecting ring is coincident




TEXT-FIG. 5. Median sections showing chamber formation cycles and cameral liquid distributions in *Nautilus*, *Paravascoceras*, and *Spirula*.

*Nautilus*: A, immediately prior to translocation. B, during translocation of the mantle. C, during secretion of the new septum thus completing the formation of chamber 'z'.

*Paravascoceras*: A, as septal secretion completed the formation of chamber 'y'. Dissolved salts were probably removed from the liquid filling chamber 'y' at this stage, while some liquid may have been expelled from chamber 'x' to compensate for mass added through continuing apertural growth. B, at commencement of translocation with possible expulsion of body liquid into the newly forming chamber space. C, during the

with septal secretion (Ward *et al.* 1981). Connecting rings have been described from the body chamber in ammonoids. Although inferred by Kulicki (1979) for *Kosmoceras* and *Quendstedtoceras*, however, such a feature has been reported only from phylloceratids (Drushchits and Doguzhayeva 1974; Kulicki 1979; Westermann 1982) and, in some cases, the connecting rings project adorally well in excess of a single chamber's length. Consequent upon his proposal of a rapid translocation rate in ammonites, Henderson (1984) suggested that the soft tissues of the siphuncle were preformed by a process of mantle invagination. The siphuncular mantle itself was thought to have been responsible for the secretion of the connecting ring following translocation. Rapid mantle movement is envisaged here only during the initial phase of translocation in *Paravascoceras*. Although partial preformation of the siphuncle may have been necessary as a consequence of this, the adoral part of the siphuncle could have formed during the latter, gradual phase of translocation.

## CONCLUSIONS

A two-stage process of mantle translocation is proposed for *Paravascoceras*. An initial phase of rapid movement, resembling that in *Nautilus*, is suggested, during which the new chamber space was flooded with liquid derived from the main body tissues. The major translocation phase, however, was a gradual process during which mantle movement kept pace with apertural growth and the new chamber space was flooded with liquid derived from the phragmocone. In this part of its chamber formation cycle *Paravascoceras* showed closer similarities to *Spirula*. The growth strategies employed by *Nautilus*, *Paravascoceras*, and *Spirula* are shown in text-fig. 5.

If other ammonoids employed the same growth strategy as *Paravascoceras*, it is possible that the relative importance of the two translocation phases varied from group to group. This might also have been the case at different ontogenetic stages within the same species. It is of interest that in their early ontogenetic stages ammonoids frequently show a morphology reminiscent of *Nautilus*, with retrochoanitic septal necks, adorally concave septa, and median siphuncles (see, for example, Spath 1950; Drushchits and Khiami 1970; Kulicki 1979).

*Nautilus* has a very slow growth rate, at least in its post-juvenile stages (Ward *et al.* 1981; Ward and Chamberlain 1983; Cochran and Landman 1984). It is, however, questionable whether the growth mechanism proposed for *Paravascoceras* was adopted to allow faster growth. Although *Nautilus* spends a much greater proportion of its chamber formation period actively involved in septal secretion than is suggested for *Paravascoceras*, it is unclear whether its overall growth strategy is necessarily linked with a slow growth rate. The rate of apertural growth in *Nautilus* is constrained by the rate at which ballast in the form of cameral liquid can be expelled. The same constraint, however, would apply if it showed a method of buoyancy control like that proposed for *Paravascoceras*; the rate of cameral liquid redistribution would also be correlated with apertural growth rates. A more efficient osmotic pump would, alone, be sufficient to remove this constraint

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gradual and lengthy phase of mantle translocation when cameral liquid was pumped from the phragmocone into the newly forming chamber space. D, at completion of translocation when septal secretion completed the formation of chamber 'z'. Levels of cameral liquid in *Paravascoceras* are assumed to have been of the same order as those suggested for ammonoids by Westermann (1975*a*, *b*), that is, filling the last one to three chambers of the phragmocone.

*Spirula*: A, after completion of chamber 'y'. At this stage dissolved salts are being removed from the liquid in this chamber. B, as the walls of chamber 'z' begin to form. C, later during the formation of chamber 'z' as liquid isosmotic with sea water fills the new chamber space and cameral liquid hyposmotic to sea water is removed from chambers 'x' and 'y'. D, at completion of chamber 'z'. Based on Denton and Gilpin-Brown (1971) and Denton (1974).

Notice that the length of the body chamber and the total amount of cameral liquid vary markedly in *Nautilus*. In *Paravascoceras* the length of the body chamber varies but little and, as in *Spirula*, the proportion of the cameral space occupied by liquid also remains approximately constant.

upon the growth rate in *Nautilus* but pumping rates are probably only one of a number of constraining factors. The chamber formation cycle in *Spirula*, nevertheless, certainly proceeds much more rapidly than in *Nautilus*. Mature animals may have a shell comprising more than thirty chambers (Denton and Gilpin-Brown 1971). Clarke (1970) estimated that *Spirula* is sexually mature at an age of 12–15 months and has a total life span of only 18–20 months. As for ammonoids, Doguzhayeva (1982), on the evidence of assumed daily growth bands, estimated that a new chamber was added about every 14 days. Landman (1983) questioned this figure, and it should be mentioned that Saunders (1983) found that widely varying periods of time are represented by growth lines in *Nautilus*. It is, however, of interest that one specimen of *Paravascoceras* shows approximately fourteen colour bands mirroring the sutural outline within one chamber (text-fig. 4). These bands seem to record posterior mantle movement.

Westermann (1975*c*), on the other hand, suggested that an adorally directed cameral liquid pressure may have played a significant role in the formation of adorally convex and fluted septa. Such a morphology could result if the posterior mantle margin was affixed to the shell wall at the lobules, as seems to have been the case in *Paravascoceras*. An adorally directed cameral liquid pressure requires a gradual translocation process.

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P. M. P. ZABORSKI
Department of Geology
University of Maiduguri
PMB 1069 Maiduguri, Nigeria

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